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QTL analysis of potato tuber dormancy

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Abstract The potential loss of chemical sprout inhibitors because of public concern over the use of pesticides underscores the desirability of breeding for long dormancy of potato (*Solanum tuberosum* L.) tubers. Quantitative trait locus (QTL) analyses were performed in reciprocal backcrosses between *S. tuberosum* and *S. berthaultii* toward defining the complexity of dormancy. *S. berthaultii* is a wild Bolivian species characterized by a short-day requirement for tuberization, long tuber dormancy, and resistance to several insect pests. RFLP alleles segregating from the recurrent parents as well as from the interspecific hybrid were monitored in two segregating progenies. We detected QTLs on nine chromosomes that affected tuber dormancy, either alone or through epistatic interactions. Alleles from the wild parent promoted dormancy, with the largest effect at a QTL on chromosome 2. Long dormancy appeared to be recessive in the backcross to *S. berthaultii* (BCB). In BCB the additive effects of dormancy QTLs accounted for 48% of the measured phenotypic variance, and adding epistatic effects to the model explained only 4% more. In contrast, additive effects explained only 16% of the variance in the backcross to *S. tuberosum* (BCT), and an additional 24% was explained by the inclusion of epistatic effects. In BCB variation at all QTLs detected was associated with RFLP alleles segregating from the hybrid parent; in BCT all QTLs except for two found through epistasis were detected through RFLP alleles segregating from the recurrent parent. At least three dormancy QTLs mapped to markers previously found to be associated with tuberization in these crosses.

Key words *Solanum tuberosum* · *Solanum berthaultii* · QTL · Potato · Dormancy

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Introduction

For more than 30 years potato (*Solanum tubersum* L.) sprouting has been controlled commercially through the use of chemical sprout inhibitors. Processing potatoes, which in many countries account for a major portion of the crop, are typically stored at relatively warm temperatures and have a particular need for sprout inhibitors. In the USA there is concern among growers and processors that chemical sprout inhibitors may be banned. If this should happen, the development of cultivars with long tuber dormancy will assume a much higher priority.

Dormancy in potato tubers, also referred to as the rest period (Hemberg 1985), will be defined here as the physiological state during which the tuber is unable to sprout (Reust 1986). Tubers with long dormancy do not sprout even if stored at warm temperatures, and this trait is quantitatively inherited (Kotch et al. 1992). A companion paper (Van den Berg et al. 1996) describes the use of two backcross populations to identify quantitative trait loci (QTLs; Tanksley et al. 1989) for potato tuberization. *S. berthaultii*, the wild species crossed to *S. tuberosum* in those studies, is noted for its long tuber dormancy (Thomson et al. 1987). Thus, the same two backcross populations were used to carry out studies on tuber dormancy.

We report here the identification of QTLs on nine chromosomes that affected tuber dormancy in our backcrosses. Epistatic effects were of major importance for many of these QTLs. At least three of the QTLs mapped to markers previously found to be associated with tuberization. We compare our results to those from a similar study on a population derived from a hybrid of diploid

S. tuberosum × *S. chacoense* crossed to *S. phureja* (Freyre et al. 1994).

Materials and methods

Plant material, plant growth conditions, and tuber storage conditions

In 1990, 299 genotypes of the backcross to *S. tuberosum* (BCT) and 288 of the backcross to *S. berthaultii* (BCB) were grown in separate experiments as described in Van den Berg et al. (1996). Tubers from one block of each experiment were saved to screen for tuber dormancy. Tuber size is reported to affect dormancy, larger tubers having a shorter dormant period (Emilsson 1949; Krijthe 1962); but the size effect differs by genotype (Van Ittersum 1992). In order to adjust for these size effects, we selected three tubers of different sizes from each plant, one each in the range of 5–10 g, 10–20 g, and 20–30 g. Plants without tubers (ca. 1%) or with only one tuber (ca. 1%) were not used for the experiment. For genotypes that lacked one size class (ca. 5% of the plants) the missing value was estimated according to a modification of the missing plot formula for a randomized complete block experiment (Snedecor and Cochran 1980), with tuber size classes as the blocks. In all experiments, large tubers had on average slightly shorter dormancy periods than the smaller tubers, but the differences were not significant.

After plant maturity, selected tubers of 237 clones of BCT were placed in the dark at a constant temperature of 13° ± 1°C. BCB tubers from 269 clones were kept in the dark at 18° ± 5°C for 40 days and for 45 days at 4° ± 1°C prior to storage at 13° ± 1°C. For each tuber in BCT and BCB we recorded the number of days from harvest until sprouts had grown to a length of 3 mm. The mean time for the three tubers constituted the dormancy value (DORM-1) for each genotype.

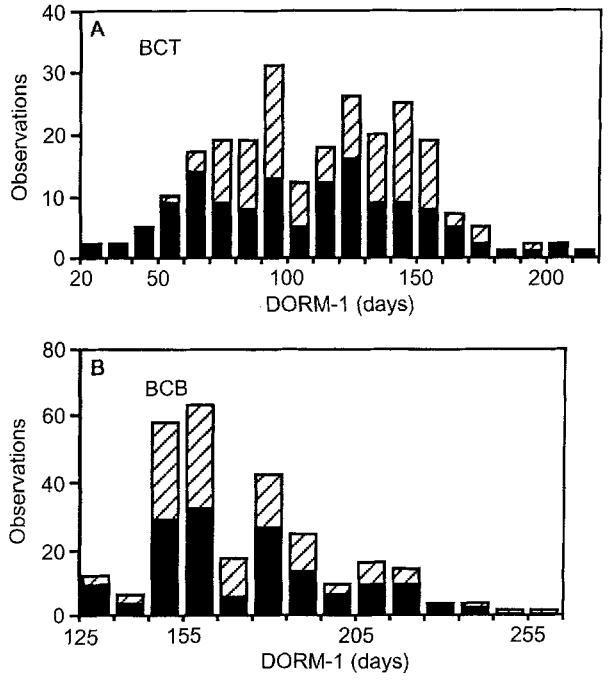

Fig. 1 A,B Frequency distributions of DORM-1 data. The total length of each *bar* represents the entire population; the *filled portion* represents the individuals taken for RFLP genotyping. The values on the *abscissa* are the midpoint values for DORM-1, the time from harvest until sprouting. **A** BCT, **B** BCB. Growing and storage conditions were different for BCT and BCB, so values for the two populations should not be compared

In 1991, 155 selected BCT clones, the hybrid parent (M200-30), and both *S. tuberosum* parents were grown together. Tuber dormancy was measured as for BCT in the previous year and is denoted DORM-2. Again, tuber size had no significant effect when all genotypes were considered together.

Restriction fragment length polymorphism (RFLP) linkage analyses

Tuber dormancy and tuberization traits were used for selective genotyping of BCT (Van den Berg et al. 1996), with emphasis on the phenotypic extremes (Fig. 1A). Because selection in BCB was based upon trichome characteristics (Bonierbale et al. 1994), there was no obvious effect on the distribution of DORM-1 (Fig. 1B). Of the clones selected for RFLP analysis in each cross, there were enough tubers to obtain DORM-1 for 147 of the 150 genotypes in BCB and 130 of the 155 genotypes in BCT. DORM-2 was based upon 126 genotypes from BCT.

In BCT restriction fragments were segregating from both the hybrid parent and the recurrent *S. tuberosum* parent. Those from the hybrid parent are designated as B alleles, those from the recurrent parent as T^R alleles. Similarly, in BCB, restriction fragments segregating from the hybrid parent and from the recurrent *S. berthaultii* parent are designated T alleles and B^R alleles, respectively. QTL analyses and significance levels were as in Van den Berg et al. (1996). Epistasis was tested among the detected QTLs with LOD scores or (−LOG[*P*-values] ≥ 1); but only those cases of epistasis are reported where the interaction for the tested traits had $P \leq 0.01$ for DORM-1 or DORM-2, or the interaction was significant at $P \leq 0.10$ for both of these traits.

Results

The dormancy measurements for clones measured in both years were significantly correlated ($r = 0.69$, $P < 0.001$). Because the plant growth conditions and tuber storage conditions were different for BCT and BCB in 1990, the means for DORM-1 from these populations should not be compared. DORM-2 for the original *S. tuberosum* parent (USW2230) was 145 days compared to 84 days for the recurrent parent (HH1-9), 188 days for the hybrid parent, and 142 days for the mean of BCT. Tubers of the *S. berthaultii* parents were not available for sprouting tests; but in our experience with this species in resistance screening and breeding, it is characterized by very long tuber dormancy.

Location and parental source of QTLs affecting tuber dormancy

QTLs were found through tests for both direct (main) effects and epistatic (interactive) effects. In BCB, all of the QTLs were detected through RFLP alleles segregating from the hybrid parent (T alleles in the *S. berthaultii* background); none were detected through the recurrent parent. In tests for direct effects, four QTLs were significant for DORM-1 in BCB (Fig. 2; Table 1). Of these a QTL at *TG234* on chromosome 2 accounted for 31% of the variance. The presence of a T allele at *TG234* decreased the length of the dormant period by 29 days (Table 1). The three other QTLs – near *TG66* on chromosome 3, *TG443* on chromosome 4, and *TG41* on chromosome 8 – had much smaller effects; but for all three, the presence of a T allele shortened dormancy.

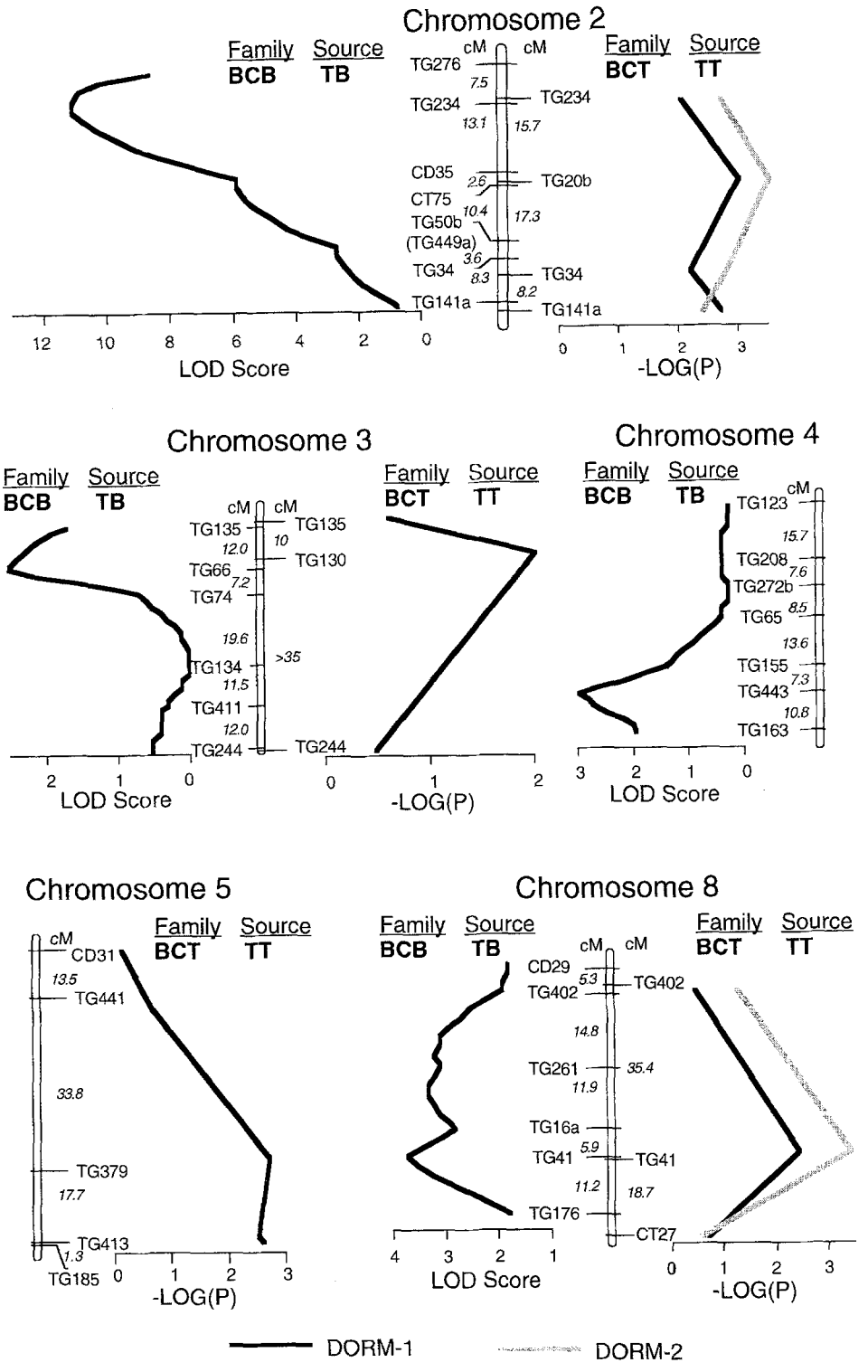

Fig. 2 Chromosome activity maps for DORM-1 and DORM-2. Maps are based on the segregation of alleles from the hybrid parent used for BCB and the recurrent parent used for BCT (Table 1). The significance levels are presented in LOD scores for alleles segregating from the hybrid, while significance levels are presented as $-\text{LOG}(P)$ scores (see Materials and methods) for alleles segregating from the recurrent parent. The datasets to which the activity curves relate are indicated by backcross family (*BCB* or *BCT*) and parental source of segregating alleles (*TB*, hybrid; *TT*, recurrent *S. tuberosum*). The effect of the different alleles at the QTLs presented in this figure are shown in Table 1. Distances in centiMorgans (cM) represent Kosambi map units based on recombination among markers in the respective parental source

The QTLs at *TG66* and *TG443* showed epistatic interactions with each other and also with a QTL at *TG497* on chromosome 11 (Fig. 3; Table 2). In all three cases of epistasis, only those genotypes that lacked a T allele at both interactive loci showed prolonged dormancy.

In contrast to BCB, segregation of RFLP alleles from the recurrent parent was very important for the detection of QTLs in BCT. This was not surprising given the relatively wide variation reported here for dormancy between our two experimental *S. tuberosum* clones (USW2230 and HH1-9). All four QTLs found for DORM-1 in tests for direct effect were detected by following T^R alleles, and two of these coincided with QTLs detected for DORM-2 (Fig. 2; Table 1). Of the four QTLs for DORM-1, three (*TG20b*, *TG130*, and *TG379*) were also involved in epistatic reactions with

Table 1 Phenotypic effects of the QTLs detected for tuber dormancy through tests for direct (main) effects

a) QTLs detected (LOD > 2.5) in BCB through segregation of T alleles from the hybrid parent (BT). Presence or absence of the T allele is indicated by + or 0, respectively

Chromosome	Locus	Presence of T	DORM-1	
			Variance explained (%)	Mean (days)
2	*TG234*	+	31	158
		0		187
3	*TG66*	+	7	166
		0		180
4	*TG443*	+	8	166
		0		181
8	*TG41*	+	10	164
		0		181

b) QTLs detected ($P \leq 0.01$) in BCT through segregation of T^R alleles from the recurrent *S. tuberosum* parent (TT). Presence or absence of the T^R allele is indicated by + or 0, respectively

Chromosome	Locus	Presence of T^R	DORM-1		DORM-2	
			Variance explained (%)	Mean (days)	Variance explained (%)	Mean (days)
2	*TG20b*	+	9	117	12	151
		0		93		128
3	*TG130*	+	5	98	n.s.[a]	–
		0		117		–
5	*TG379*	+	7	97	n.s.	–
		0		119		–
8	*TG41*	+	6	121	10	157
		0		99		134

[a] n.s., Not significant at $P \leq 0.01$

QTLs detected by segregation from either the hybrid parent (Table 3) or the recurrent parent (Table 4). Additional QTLs were found on four other chromosomes only through epistasis analysis. These were QTLs linked to *TG116*, *TG65*, *TG254*, and *CT124*, on chromosomes 1, 4, 9, and 10, respectively (Figs. 2 and 3; Tables 3 and 4). Because there was only 1 marker with segregating T^R alleles on chromosome 1, it is not possible to say where on the chromosome the QTL linked to *TG116* was located.

Chromosomes with more than one significant allelic effect

In one case of apparent epistasis, the QTLs involved were both on chromosome 2, where there was an interaction between *TG449a* and *TG20b* (Table 3). The first marker is from the hybrid parent; the second is from the recurrent parent, for which the markers are more widely spaced. Hence, both markers could be tagging a common QTL. If so, the apparent interaction between two QTLs actually reflects four distinct genotypes associated with a single QTL. By this scenario there were at least three alleles at the locus, and longest dormancy was associated with the presence of BT^R.

Further complicating matters, there was an interaction in BCT between a QTL near *TG276* on chromosome 2, detected in segregation from the hybrid parent, and one near *TG65* on chromosome 4, detected in segregation from the recurrent parent (Table 3). *TG276* is close to *TG234*, where the QTL with the largest effect in BCB was located. Thus, the 2 markers may well tag the same QTL, which may or may not be distinct from the one(s) tagged by *TG449a* and *TG20b*. Fine mapping in subsequent generations of the interspecific progeny would enhance the resolution of these genetic effects.

There were other occurrences of a QTL in one backcross that might have been the same as a QTL found in the other backcross. On chromosome 3 the QTL at *TG130* in BCT was close to the QTL at *TG66* in BCB, and QTLs in both backcrosses were linked to *TG41* on chromosome 8 (Fig. 2). A T allele on chromosome 8 in BCB reduced dormancy, and a T^R in BCT increased dormancy (Table 1). Either there are three different alleles segregating at *TG41*, or the T^R allele is the same as the B allele. A second apparent peak in the activity curve in BCB was found on chromosome 8 at *TG261* (Fig. 2). It is unclear whether this peak constitutes another QTL on chromosome 8. On chromosome 4 there were only 3 markers with segregating T^R alleles, too few to determine whether the QTL found at *TG65* by epistasis (Table 3) was distinct from the QTL tagged by *TG443* in BCB (Fig. 2).

In summary, although we cannot be confident that there was more than one QTL on any one chromosome,

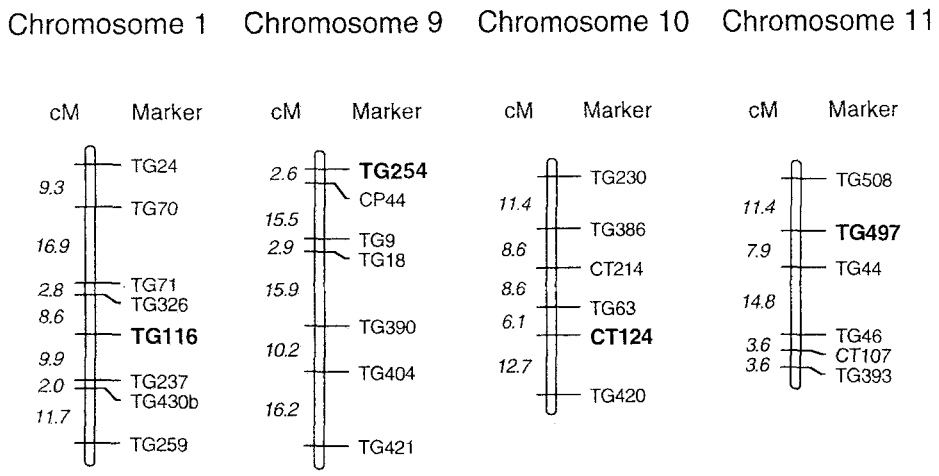

Fig. 3 Location of QTLs detected through epistasis on chromosomes for which no main effects were detected. A QTL linked to *TG497* (chromosome 11) was detected for DORM-1 in BCB (Table 2). QTLs detected for DORM-1 and DORM-2 in BCT (Table 4) were linked to *TG116* (chromosome 1), *TG254* (chromosome 9), and *CT124* (chromosome 10). However, the location of the QTL linked to *TG116* is unresolved because there was only one marker with segregating T^R alleles on chromosome 1

Table 2 Interactions (epistasis) in BCB between two loci, both of which had T alleles segregating from the hybrid parent (BT). The presence or absence of a T allele at each locus is indicated by + or 0, respectively. All interactions were significant at $P \leq 0.01$

Locus and Presence of T	Locus and Presence of T	DORM-1 (days)
TG66(3)[a]	*TG443*(4)	
+	+	165
+	0	167
0	+	168
0	0	189
TG66(3)	*TG497*(11)	
+	+	167
+	0	165
0	+	170
0	0	187
TG443(4)	*TG497*(11)	
+	+	168
+	0	165
0	+	169
0	0	189

[a] (Chromosome number)

at least nine QTLs on nine chromosomes affected tuber dormancy in our crosses. The QTLs found in BCB explained 52% of the variance for DORM-1 if epistatic effects were included in the regression model, and 48% if they were not included. In contrast, in BCT 40% of the variance for DORM-1 was explained with epistasis included, and 16% without. The equivalent values for DORM-2 were 40% and 17%, respectively.

Discussion

Source and dominance of favorable alleles

S. berthaultii appears to provide promising germplasm for increased tuber dormancy. The QTL detected in BCB near marker *TG234* on chromosome 2 had a major effect (Fig. 2; Table 1), explaining 31% of the variance. The dormant period was shortened by 29 days when a T allele was present at this marker. The QTL with the largest effect on dormancy in BCT was detected at

Table 3 Interactions (epistasis) in BCT between one locus that had B alleles segregating from the hybrid parent (BT) with another locus that had T^R alleles segregating from the recurrent parent (TT). The presence or absence of a B allele at the first locus is indicated by + or 0, respectively. The presence or absence of a T^R allele at the second locus is similarly designated. Interactions presented are those where: (1) at least one trait tested had $P \leq 0.01$ or (2) both DORM-1 and DORM-2 were significant at the $P \leq 0.1$ level

Locus and presence of B	Locus and presence of T^R	DORM-1 (days)	DORM-2 (days)
TG449a(2)[a]	*TG20b*(2)		
+	+	129	160
+	0	94	128
0	+	101	138
0	0	91	128
(Significance)		(0.08)	(0.08)
TG276(2)	*TG65*(4)		
+	+	132	160
+	0	102	142
0	+	93	139
0	0	98	130
(Significance)		(0.08)	(0.08)

[a] (Chromosome number)

Table 4 Interactions (epistasis) in BCT between two loci, both of which had T^R alleles segregating from the recurrent *S. tuberosum* parent (TT). The presence or absence of a T^R allele at each locus is indicated by + or 0, respectively. Interactions presented are those where: (1) at least one trait tested had $P \leq 0.01$ or (2) both DORM-1 and DORM-2 were significant at the $P \leq 0.1$ level

Locus and presence of T^R		Locus and presence of T^R	DORM-1 (days)	DORM-2 (days)
TG116(1)[a]		*TG379*(5)		
+		+	108	149
+		0	119	141
0		+	84	126
0		0	119	154
	(Significance)		(0.08)	(< 0.01)
TG20b(2)		*TG254*(9)		
+		+	105	144
+		0	128	156
0		+	96	134
0		0	89	121
	(Significance)		(0.05)	(0.05)
TG20b(2)		*CT124*(10)		
+		+	125	155
+		0	107	145
0		+	88	120
0		0	97	141
	(Significance)		(0.09)	(0.02)
TG130(3)		*TG379*(5)		
+		+	83	–
+		0	120	–
0		+	115	–
0		0	118	–
	(Significance)		(< 0.01)	(n.s.)[b]
TG254(9)		*CT124*(10)		
+		+	98	135
+		0	102	147
0		+	125	152
0		0	101	136
	(Significance)		(0.08)	(0.04)

[a] (Chromosome number)
[b] n.s., Not significant at $P \leq 0.1$

approximately the same place on chromosome 2 and may be identical. All five of the alleles promoting long dormancy in BCB, including the one found only through epistasis (Table 2), were B alleles. This was to be expected, inasmuch as *S. berthaultii* is known for its long dormancy.

There were also substantial differences in dormancy within *S. tuberosum*. The first *S. tuberosum* parent had a considerably longer dormant period than the *S. tuberosum* parent used to make the backcross. We therefore expected that at any QTL detected in BCT through alleles segregating from the recurrent parent, short dormancy would be conferred by T^R. This was the case for QTLs on chromosomes 3 and 5; but at two of the QTLs detected in BCT, T^R prolonged dormancy (Table 1). Furthermore, in five cases the presence of T^R at one QTL prolonged dormancy in combination with a T or B allele at another QTL (Tables 3 and 4). For the epistasis found between *TG20b* and *CT124*, T^R alleles at *both* markers yielded the longest dormancy. It is not unusual that genes favoring a trait are segregating from a phenotypically unfavorable parent, a type of transgressive segregation illustrated by deVincente and Tanksley (1993). Freyre et al. (1994) also found transgressive segregation in their investigation of potato tuber dormancy. In the present study the phenomenon was most evident when epistasis was considered.

For progenies resulting from crosses between heterozygous individuals, these findings emphasize the importance of examining alleles segregating from the recurrent parent as well as from the hybrid parent. They also illustrate the importance of considering epistatic relationships and the particular genetic background in which an effect is measured. In BCT the variance explained by inclusion of epistatic effects in the regression model was 2.5 times that explained when only direct effects were included. Although only three cases of epistasis were detected in BCB, it is interesting that for all three cases, long dormancy required that two *S. berthaultii* alleles be present at both QTLs involved in the interaction.

In BCB the absence of T also prolonged dormancy for all four QTLs detected by examining direct effects, whereas no QTL in BCT was found for direct effects of B alleles segregating from the hybrid parent. When all the evidence is considered, it seems likely that long dormancy is recessive at the QTLs found in BCB. However, epistatic interaction in BCT complicates the interpretation (Table 3, *TG276* × *TG65*).

Comparison with earlier published results

Although there were too few common markers between the two studies to permit precise comparisons, it is useful to compare the QTLs found in our work with QTLs reported for tuber dormancy when a hybrid between a haploid of *S. tuberosum* × *S. chacoense* was crossed with *S. phureja* (Freyre et al. 1994). *S. berthaultii*, used in our experiments, has much longer dormancy than *S. tuber-*

osum; in contrast, *S. phureja* has a much shorter dormancy than *S. tuberosum*. Freyre et al. (1994) suggested that *S. phureja* contributed dominant genes for short dormancy; our data indicate that *S. berthaultii* contributed recessive genes for long dormancy.

As might be expected from studies involving different species, some of the QTLs found were different between the two studies; but several were close enough that they are likely the same. The five chromosomes upon which we detected QTLs for dormancy were the same as five of the six chromosomes reported by Freyre et al. (1994); but we detected no QTLs on chromosome 7, which contained the most important QTLs for segregation from the *S. tuberosum* × *S. chacoense* hybrid. Another difference was that the most important QTL in BCB was near marker *TG234* on chromosome 2; whereas in the segregation from *S. tuberosum* × *S. chacoense*, nothing was detected near this locus (Freyre et al. 1994). However, there was a significant QTL in BCT at *TG34* on chromosome 2 that may be near two QTLs found by Freyre et al. (1994). The QTLs on chromosomes 3 and 8 appear to be at similar locations between the two studies, and this may well be true of the QTLs on chromosome 5. On chromosome 4 the QTL found in BCB near *TG443* seems to be well-separated from the one reported on chromosome 4 by Freyre et al. (1994), but it is diffcult to say whether the latter is distinct from a QTL found in BCT near *TG65*.

Ahn et al. (1993) inferred orthology of genes influencing morphology in rice, wheat, and maize based on their location within conserved segments of the respective genomes. Comparative QTL mapping similarly provides the means to determine whether different species – or genera – carry the same or different components of genetic variability for the traits of interest.

Pleiotropic effects with tuberization

The ending of tuber dormancy is associated with a decrease in endogenous acidic inhibitors, among which is abscisic acid (Coleman and King 1984); and there is some evidence for an increase in gibberellins at this stage (Hemberg 1985). Likewise, gibberellic acid applied to dormant tubers tends to promote sprouting, whereas the application of abscisic acid tends to delay it (Hemberg 1985). A similar relationship between gibberellins and growth inhibitors is often hypothesized to explain the process of tuber initiation on potato plants. Gibberellins delay or prevent tuber initiation, and growth inhibitors such as abscisic acid have been associated with the promotion of tuber formation (Ewing and Struik 1992).

In view of the hypothesized roles of hormones in the two processes, it is striking that QTLs for dormancy detected on chromosomes 3, 4, and 8 mapped to the same markers (*TG130*, *TG65*, and *TG41*, respectively) as QTLs with effects on ability to tuberize under long days (Van den Berg et al. 1996). Moreover, on chromosomes 4 and 8 the absence and on chromosome 3 the presence of T^R were associated with both earlier tuberization and shortened dormancy. These responses are what one might expect if genes at these QTLs are mediating gibberellins in such a manner as to both restrict tuberization and shorten dormancy, or if they are mediating levels of inhibitory hormones that have the opposite effects. At the resolution employed in our experiments, these relationships could be due to either pleiotropy or linkage. The observed concurrence of our results with what might be expected from our physiological understanding of the relationships suggests pleiotropy, but proof would require finer mapping in subsequent generations or association of a single gene product with both phenotypes. To further investigate the biochemical basis for these putative pleiotropic effects, we are carrying out hormonal analyses for the plants in BCT so that any QTLs found for hormones can be compared to those found for dormancy and tuberization.

Implications for breeding

The enormous range in tuber dormancy among species offers the potential for customizing the dormant period of new cultivars according to need. A comparison of our results to those of Freyre et al. (1994) suggests that one cannot assume that the genetic control of tuber dormancy is the same in all *Solanum* species, with only modifications in degree. It may be that the large effect reported by Freyre et al. (1994) for chromosome 7 came from the *S. chacoense* parent used in their pedigree, though it would be necessary to combine the respective gene pools to investigate thoroughly the genetic control. *S. chacoense* is generally considered to possess long tuber dormancy (R.E. Hanneman, Jr., personal communication). It would be interesting to bring the loci found by Freyre et al. (1994) into our populations, and the loci contributed by *S. berthaultii* (especially on chromosome 2) into theirs.

Tuber dormancy is desirable when potatoes are stored; however, excessively long dormancy poses a problem in sprouting of seed tubers. An extreme example is the situtation in North African countries where two or even three crops of potatoes are grown in 1 year. Tubers harvested in one season are used as seed for the succeeding crop. Thus, the right dormant period for one environment or purpose may be wrong for another one. The availability of several alleles with various effects on dormancy gives the breeder the opportunity to fine-tune the dormant period of a new variety according to need. This would be facilitated by the use of QTL mapping.

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